

J. MEESTER

TRANSSVAAL MUSEUM,  
PRETORIA.

The distribution  
of *Crocidura* Wagler  
in Southern Africa

The present paper summarizes the zoogeographic results obtained from a systematic revision of the genus *Crocidura* Wagler in southern Africa. The data on which these results are based form part of a more extensive report which is being published elsewhere (Meester, in press), and will not be repeated here in full. Keay's (1959) classification of vegetation types is followed. Rainfall distribution is taken from Wellington (1955).

Nine species are recognised: *Crocidura flavescens* (I. Geoffroy), *C. occidentalis* (Pucheran), *C. cyanea* (Duvernoy), *C. silacea* Thomas, *C. hirta* Peters, *C. luna* Dollman, *C. pilosa* Dobson, *C. bicolor* Bocage, and *C. maquassiensis* Roberts.

*C. flavescens* ranges from the south-western Cape Province, along the coast to the Eastern Province, inland to Lady Grey and perhaps Burgersdorp, further north along the coast to Durban district, and thence inland to the Maluti mountains in Basutoland and the Sabie district, eastern Transvaal (Fig. 1). A similar distribution pattern has been found in the case of various other species, such as *Myosorex varius* (Meester 1958: 326), *Amplorhinus multi-maculatus*, the many-spotted snake, *Lycodonomorphus laevis*, the African water snake, and *Philothamnus natalensis*, the Natal green water snake (Dr. Y. F. FitzSimons, in litt.).

The range of *C. flavescens* falls entirely within the rainfall zone with an annual mean of 20 in. and over, with the exception of the dubious record from Burgersdorp. Most known localities further fall within the zone of 30 in. and over, and it appears that the colour of *C. flavescens* varies in response to variation in moisture conditions, being darker on the whole in the 30-plus in. zone than in the 20-30 in. zone.

No relationship is apparent with vegetation type. However, whatever vegetation type it inhabits, *C. flavescens* appears to frequent dense cover. For the rest it is normally found in broken country. On the eastern escarpment of the eastern Transvaal it ranges no further than the Sabie district, north of which, in the Olifants river valley, there is a break in the escarpment which may constitute a barrier to its spread. In the northern Transvaal and south-eastern Southern Rhodesia there is a more extensive break in the eastern escarpment, with lower rainfall (10-20 in. per annum) and different vegetation type from that found towards either the south or the north (woodland and savanna with abundant *Colophospermum mopane* —Keay 1959). This break doubtless prevents its ranging further north, and probably also acts as a barrier to the southward spread of *C. luna* and *C. occidentalis* (Fig. 2).

*C. luna* is confined in southern Africa to the eastern escarpment of Southern Rhodesia, where it extends as far south as the Melsetter district. *C. occidentalis* is sympatric with it in this area, and is further found at Mbambi on the Okavango. Both species are restricted to

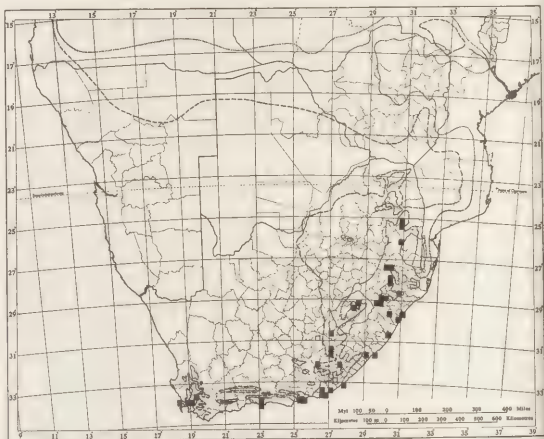


Fig. 1: Distribution of *Crocidura flavescens*. Solid squares represent authenticated records; dubious or literature records are represented by open squares. Broken line = 20 in. mean annual rainfall zone; dotted line = 30 in. mean annual rainfall zone.

a moist environment. Where they occur in Southern Rhodesia, mean annual rainfall is above 40 in. and, while the Okavango River runs through a drier area with a mean annual fall of 20–30 in., the habitat occupied by *C. occidentalis* (swamp vegetation) should meet the environmental requirements of a moisture-restricted species.

To these two species, perhaps even more than to *C. flavescens*, the dry conditions (and perhaps the different vegetation type) of the break in the eastern escarpment would constitute an effective barrier.

The failure of *C. occidentalis* to range further south in the western part of its southern African range can probably be explained on the same grounds. The Okavango runs through an only moderately moist area. Further south rainfall drops still further, to 10–20 in. per annum, and south of the Okavango swamp and Lake Ngami it would be impossible for this species to satisfy its environmental requirements by inhabiting the moist habitat offered by riverine or swamp vegetation. Probably, therefore, here as along the eastern escarpment it is prevented from ranging further south by the arid conditions it would encounter.

# THE DISTRIBUTION OF CROCIDURA WAGLER IN SOUTHERN AFRICA

*C. hirta* extends from the extreme northern Cape Province in the west and Durban in the east, through Bechuanaland, north-eastern South West Africa, the Transvaal, Moçambique and Southern Rhodesia, to the Kunene and Zambezi rivers, and thence further north (Fig. 3). *C. bicolor* appears to have a roughly similar distribution, although locality records are few and scattered, and do not extend quite as far south as in the case of the other species. Neither species is represented in the extremely dry western part of South West Africa, with rainfall much below 8 in. (200 mm.) per annum.

In both *C. hirta* and *C. bicolor* colour variation in response to variation in moisture conditions has led to the establishment of moisture-adapted subspecies, a paler western dry-area form (*C. h. deserti* and *C. b. woosnami*), and a darker eastern moist-area form (*C. h. hirta* and *C. b. bicolor*). In both cases, furthermore, the subspecies boundary coincides roughly with the 20-in. or the 24-in. (600 mm.) mean annual rainfall zone (see also Meester 1959).

The eastern subspecies (particularly the widespread *C. h. hirta*) occupy diverse vegetation types, but mainly woodland and savanna; the western subspecies inhabit partly relatively dry,

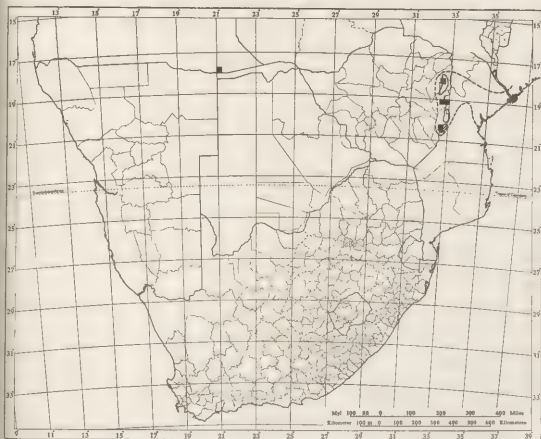


Fig. 2: Distribution of *Crocidura occidentalis* in southern Africa. Broken line = 40 in. mean annual rainfall zone; dotted line = 60 in. mean annual rainfall zone.

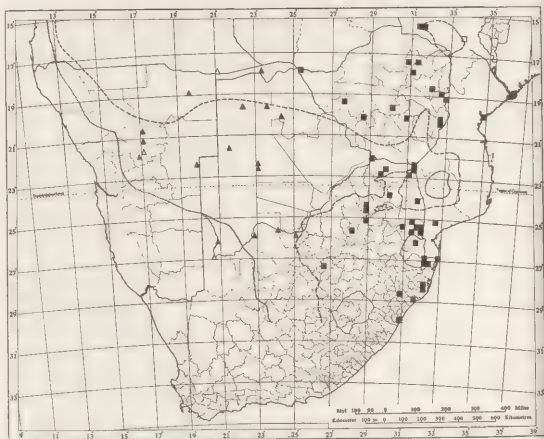


Fig. 3: Distribution of *Crocidura hirta* in southern Africa. Squares = *C. h. hirta*; triangles = *C. h. deserti*. Solid symbols represent authenticated records, while open symbols represent dubious or literature records. Dotted line = 10 in. mean annual rainfall zone; broken line = 20 in. mean annual rainfall zone.

undifferentiated woodland and savanna, and partly wooded steppe with abundant *Acacia* and *Commiphora* (Keay 1959).

*C. cyanea* has an extensive range in southern Africa, extending all the way from the Cape Peninsula to the Kunene and Zambezi rivers, with the exception only of the Namib Desert, with mean annual rainfall less than 5 in. It is unknown from some areas within this region, such as parts of the northern Cape Province, the Kalahari and Bechuanaland, but this may be the consequence merely of gaps in our knowledge of its distribution (Fig. 4).

In this species too, adaptation in response to variation in moisture conditions has led to the establishment of dry- and moist-area subspecies, and again the boundaries of the subspecies meet, where they do so, along the 20-in. mean annual rainfall zone. (In parts of their ranges the two subspecies are apparently geographically isolated, at least on present evidence). However, in this case the western arid-area form, *C. c. cyanea*, is only slightly paler than the eastern form, *C. c. infumata*, and differs mainly in being more grey and grizzled than the latter.

# THE DISTRIBUTION OF CROCIDURA WAGLER IN SOUTHERN AFRICA

*C. silacea* ranges from Natal and Zululand to Swaziland, northward along the eastern escarpment to eastern and northern Transvaal, westward to the Pretoria district, the Transvaal highveld and Kanje, Bechuanaland, and further north to Southern Rhodesia and beyond. This range includes the three known records for *C. maquassiensis*, which may be the same animal. All available locality records for both species fall within the mean annual rainfall zone of 20 in. and over. Towards the south its range is limited in somewhat the same fashion as that of *C. h. hirta*.

*C. pilosa* occurs in southern Africa in two geographically completely isolated regions, in which two different subspecies are recognized (Fig. 5). *C. p. pilosa* ranges from Inhambane, Moçambique, to Mooi River, Natal in the south, and to Woodbush, northern Transvaal, Potchefstroom, Transvaal highveld, and Vredefort, Orange Free State in the west. An unconfirmed but probably authentic record further suggests that its range extends as far west as the junction of the Marico and Limpopo rivers.

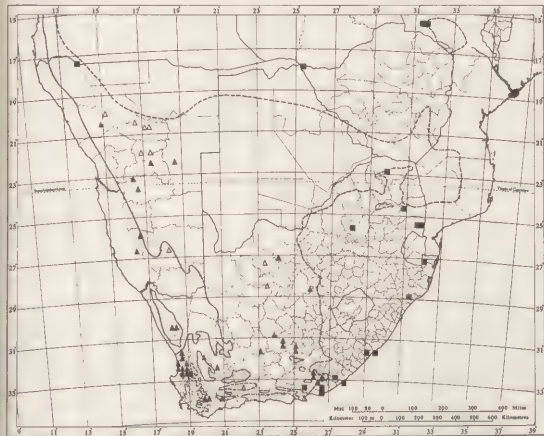


Fig. 4: Distribution of *Crocidura cyanea* in southern Africa. Triangles = *C. c. cyanea*; squares = *C. c. infumata*. Solid symbols represent authenticated records; dubious or literature records are represented by open symbols. Dotted line = 5 in. mean annual rainfall zone; broken line = 20 in. mean annual rainfall zone.

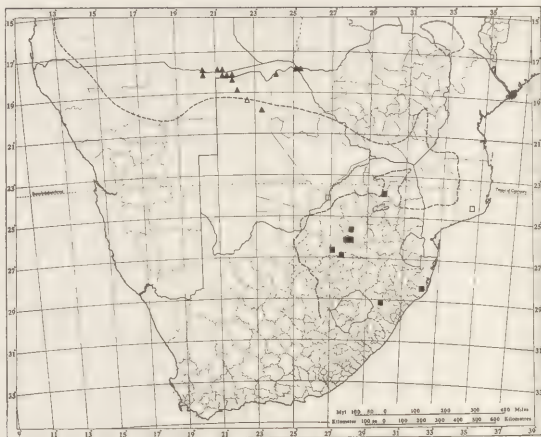


Fig. 5: Distribution of *Crocidura pilosa* in southern Africa. Squares = *C. p. pilosa*; triangles = *C. p. shortridgei*. Solid symbols represent authenticated records, while dubious or literature records are represented by open symbols. Broken line = 20 in. mean annual rainfall zone.

*C. p. shortridgei* is known in Southern Africa from the Okavango river in north-eastern South West Africa, the Caprivi strip and Ngamiland, and has also been collected in parts of Northern Rhodesia. This form is restricted roughly to the rainfall zone with an annual mean of 20 in. and over and so, apparently, is *C. p. pilosa*. Both subspecies occupy a moist environment. The geographic gap between their ranges, extending across the Kalahari desert and northern Bechuanaland, consists of a zone with lower rainfall (10–20 in. per annum), lacking the moist environmental conditions they appear to require. This suggests that their geographic isolation may be associated with an ecological barrier in moisture conditions extending across this area.

It is not clear why *C. pilosa* does not occur in Southern Rhodesia, where favourable environmental conditions for its survival would appear to prevail. It is further not clear why this species, and also *C. hirta*, *C. bicolor* and *C. silacea*, range no further south than they do. They do not appear to be limited by either rainfall, vegetation or topographic barriers; indeed the eastern coastal belt forms a corridor for the southward spread of a number of

species, like *C. flavescens*, *Myosorex varius*, *M. cafer* (see Meester, 1958) and others. *C. pilosa* and *C. silacea* have a somewhat restricted range, and *C. bicolor*, although widespread, is not a very common species. *C. hirta*, however, not only occurs throughout a wide range of environmental conditions, but is the most common species of *Crocidura* in those areas in southern Africa where it is found. Why this species, at least, spreads no further south remains a mystery.

From the above it appears that *Crocidura* is very widespread in southern Africa, and that it occupies a variety of habitats, ranging from the extremely moist eastern escarpment of Southern Rhodesia, in parts of which mean annual rainfall exceeds 60 in., to the dry west, in areas with mean annual rainfall between 5 and 10 in. The only part of southern Africa whence it has not been recorded is the Namib Desert of South West Africa, with mean annual rainfall less than 5 in.

A widespread distribution of this nature might suggest a group that is little affected by environmental conditions. However, in fact it appears that environmental factors, notably moisture, play a prominent part in determining the distribution and nature of the species dealt with. Particularly a zone corresponding roughly with the 20-in. mean annual rainfall zone (or the 24-in. (600 mm.) zone, which follows more or less the same course), appears to be of great importance. Of the forms considered only *C. c. cyanea*, *C. h. deserti* and *C. b. woosnami* occur extensively in the below 20-in. zone, while *C. flavescens*, *C. silacea*, *C. pilosa* and the subspecies *C. c. infumata*, *C. h. hirta* and *C. b. bicolor* are virtually or entirely restricted to the zones above 20- or 24-in. In *C. cyanea*, *C. hirta* and *C. bicolor*, furthermore, in each of which one of the two recognized subspecies is a dry-area form (*C. c. cyanea*, *C. h. deserti* and *C. b. woosnami*), while the other occurs in moister areas (*C. c. infumata*, *C. h. hirta* and *C. b. bicolor*), the boundaries between subspecies coincide roughly with the 20- or 24-in. zone. In *C. pilosa* the two subspecies *C. p. pilosa* and *C. p. shorridgei* are both confined roughly to the 20-in. zone, and the intervening area with lower rainfall (10-20 in. per annum) appears to act as an ecological barrier.

*C. luna* and *C. occidentalis* appear to be restricted to an even moister environment, with mean annual rainfall above 40 in. (except where *C. occidentalis* occurs along the Okavango, in a very moist habitat). This may to some extent be true also of *C. flavescens* as this species, although occurring in the 20-30 in. zone, is for the most part found in the 30-in. zone.

In view of the important rôle of moisture in determining range limits, it is not surprising to find that it is also responsible for some variation in colour in several species. In *C. flavescens* colour is darker in the 30-in. zone than in the 20-30-in. zone. The same is the case in *C. h. hirta*. In *C. hirta* and *C. bicolor*, furthermore, the dry-area subspecies (*C. h. deserti* and *C. b. woosnami*) is in each case strikingly paler than the moist-area form (*C. h. hirta* and *C. b. bicolor*).

Thus, all three species illustrate Gloger's rule, that colour is darker in warm, moist areas than in cold or arid regions. In *C. cyanea*, however, although the dry-area form (*C. c. cyanea*) is slightly paler than that from the moister region (*C. c. infumata*) the main difference between the two forms is that *C. c. cyanea* is greyer and more grizzled than *C. c. infumata*. Doubtless this also represents an adaptation to variation in moisture conditions, following however an unusual pattern.

To some extent the forms here considered are associated with particular vegetation types, but this is probably a consequence merely of the fact that these vegetation types are similarly restricted to particular rainfall zones. Broadly speaking the western steppe country of southern Africa falls within the 5-20-in. mean annual rainfall zone, while in the 20-plus-in. zone the vegetation type is mainly temperate and subtropical grassland or woodland and savanna, with specialized types occurring in certain areas, such as high mountains and the coastal regions (Keay 1959). The forms occurring in the 5-20-in. zone, therefore, are found mainly

in steppe country, while those occurring in the 20-in. zone inhabit woodland and savanna, temperate and subtropical grassland, montane forests, the coastal forest-savanna mosaic, and the like.

*C. flavescens*, *C. luna* and *C. occidentalis* (in part) appear to be confined to mountainous regions, such as the eastern escarpment. However, this may be merely a consequence of moisture-restriction and perhaps a preference for dense cover. Both requirements would be met by the moist conditions and lush vegetation of the eastern escarpment, and particularly of the densely-vegetated mountain streams found along it.

It thus appears that the wide distribution of *Crociodura* in southern Africa is a consequence not of its being little affected by environmental factors, but of its success in adapting to these factors. Of the known forms only *C. flavescens* and possibly *C. maguassiensis* (if it is a valid species) may have originated locally. The other species almost certainly colonized southern Africa from East and Central Africa. As such they were probably all adapted to an at least moderately moist environment (with mean annual rainfall above about 20 in.), as indeed is the case with most of the forms at present known from southern Africa. The forms occurring in dry areas (*C. h. deserti*, *C. b. woosnami* and *C. c. cyanea*) therefore probably represent secondary adaptations to arid conditions, arising from stocks which were primarily adapted to a moister environment.

#### REFERENCES

- KEAY, R. W. J. 1959. Vegetation map of Africa south of the Tropic of Cancer . . . London. Oxford University Press, 24 pp.  
 MEESTER, J. 1958. Variation in the shrew genus *Myosorex* in Southern Africa. *J. Mammal.* 39: 325-339.  
 MEESTER, J. 1959. Adaptation of *Crociodura hirta* Peters to variation in moisture conditions in Southern Africa. *Koedoe* 2: 173-179.  
 MEESTER, J. in press: A systematic revision of the shrew genus *Crociodura* in Southern Africa. D.Sc. thesis, Pretoria University, for publication as a *Mem. Transvaal Mus.*  
 WELLINGTON, J. H. 1955. Southern Africa: a geographical study. Cambridge University Press, 2 v.

#### DISCUSSION

- Dr. Poynton*: It seems possible that the limits of distribution in some of the northern *Crociodurids* may be related to temperature and it might therefore be useful to consult an isotherm map.  
*Dr. Meester*: I have done so, but so far no close correlation emerges.  
*Dr. Stuckenberg*: What fossil record is there or other evidence of similar species occurring in the Pleistocene?  
*Dr. Meester*: There are some similar species to be found at Taung and some at Sterkfontein. *Crociodura hirta* occurs at Taung in the Middle Stone Age strata.  
*Prof. Ever*: Is there any clear specificity in feeding habits which might explain distribution?  
*Dr. Meester*: This is difficult to determine. Stomach contents are generally too well digested to yield many identifiable chitinous fragments and in some limited work on captive animals it has proved easier to discover what they do not eat than what they do.